Fire Alters Emergence of Invasive Plant Species from Soil Surface-Deposited Seeds

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Restoration of historic fire regimes is complicated by concerns about exotic plant invasions, yet little is known of how the two may interact. Seeds of Japanese brome, spotted knapweed, Russian knapweed, and leafy spurge were subjected to fire at six fuel loads (100 to 700 g m^{-2}) and a nonburned control. Fires were simulated with field-cured grass and time–temperature profiles were developed from thermocouples at the soil surface. Emergence was determined by species and fuel load in growth chambers. Fuel load explained 98% of variation in mean heat dosage and emergence decreased with increasing fuel load across species. Emergence was reduced 79 to 88% relative to nonburned treatment with 100 g m^{-2} of fuel and at least 97% with 200 g m^{-2} of fuel. Emergence probabilities were less than 0.01 for all species but spotted knapweed with a 300 g m^{-2} fuel load. Results indicate high potential for fire to disrupt the life cycle of invasive species through direct seed mortality. The relationship between fuel load and seedling emergence provides good predictability of fire effects on surface-deposited seeds. A single fire is unlikely to eradicate many invasive species because they often produce abundant seeds and some will undoubtedly escape fire. However, abrupt reductions in seedling emergence with relatively light fuel loads indicate that fire may be an effective tool for increasing mortality of invasive plant seed across a broad range of habitats.

Nomenclature: Japanese brome, *Bromus japonicus* Thunb. ex Murr.; spotted knapweed, *Centaurea maculosa* Lam.; Russian knapweed, *Acroptilon repens* (L.) DC; leafy spurge, *Euphorbia esula* L.

Key words: Germination, grassland, invasion, prescribed burning, seed mortality.

Initial introductions of many invasive plant species were concurrent with major disruptions in natural fire regimes through anthropogenic suppression and landscape fragmentation. Now that fire is better recognized as an important process for shaping plant communities (Axelrod 1985), there is increased interest in using fire to restore ecosystem structure and function. Recently, a change in invasive plant management strategies has been called for whereby emphasis on management of individual invasive species is reduced and more attention is focused on addressing invasion processes through restoration of ecosystem function (Hulme 2006). However, interactions between fire (prescribed or wild) and invasive species need to be characterized before fire regimes can be restored because establishment of nonnative plants has become a concern worldwide.

Prevalent theory and empiricism indicate that elevated resource availabilities will encourage exotic plant invasion (Davis et al. 2000; Davis and Pelsor 2001) and dominance after invasion (Burke and Grime 1996; Huenneke et al. 1990). Resource availabilities increase when disturbances reduce resource uptake by the resident community (Thompson et al. 2001) and when resource supplies increase because of processes such as atmospheric nitrogen deposition (Vitousek et al. 1997). Because fire can simultaneously decrease resource uptake by temporarily reducing live biomass and increase resource supply, such as inorganic nitrogen availability (Pyne et al. 1996), one could easily assume fire to be the consummate example of an invasion-promoting disturbance. However, propagules must be available to utilize additional resources released by fire (Davis et al. 2000). Therefore, seeds and meristems must first avoid heat damage and combustion.

Lethality of fire is dependent on magnitude of heat as it interacts with duration of exposure and insulating characteristics of the tissue and its immediate environment. Although the chemical and physical effects of fire are complex, both magnitude and duration of heat are generally related to the amount of combustible fuel (Laterra et al. 2006; Wright et al. 1976) and more specifically to the amount of fuel fully combusted (Bradstock and Auld 1995). Lethal levels of heat exposure have been determined for tissues of some plant species (Levitt 1972; Whelan 1995; Wright and Bailey 1982) and fire intensity has been identified as a controlling factor in postfire germination of fire-dependent species (Keeley 1987; Mucunguzi and Oryem-Origa 1996; Thanos and Rundel 1995). However, most invasive species are not fire dependent and determination of lethal heat dosage has generally been based on fixed temperatures and durations. Controlled experiments on invasive species' seed response to actual fire are lacking despite the importance of seed availability for successful colonization and recent calls for such investigation (Emery and Gross 2005; Prober et al. 2005).

The relative abundance of invasive plants following fire has been variable, with both increases and decreases being reported (DiTomaso et al. 2006). In cases where fire has discouraged invading species, the target species was often very reliant on seeds for population maintenance and a large proportion of seeds was believed killed by the fire (DiTomaso et al. 2006; Emery and Gross 2005; MacDonald et al. 2007; Prober et al. 2005). Thus it appears that fire effects on resource availabilities are sometimes counterbalanced by fire-induced seed mortality.

Annual species with short-lived seed banks are the most likely candidates for control with fire alone, but seed banks of plants with other life histories may be reduced if the plants are burned while seeds are vulnerable to heat damage (DiTomaso et al. 2006; Gleadow and Narayan 2007). Although the biology of invasive plants varies considerably among species, an abundance of propagules is required for successful invasion (Grime 2001) and most invasive species rely on seed for initial

colonization and continued expansion. The potential that fire sometimes discourages invasive species by killing appreciable numbers of seeds makes it imperative that conditions under which this occurs be determined to facilitate restoration and prevent invasions. If invasive plant seed mortality is directly related to fire intensity, fuel load may provide easily attainable estimates of impacts after wildfire and conditions could be manipulated to favor seed mortality of potential invading species with prescribed fire.

The research objective was to determine fire effects on emergence of the invasive plants Japanese brome, spotted knapweed, Russian knapweed, and leafy spurge across a range of common grassland fuel loads. These species represent a range of reproductive strategies, with an annual grass (Japanese brome) and perennial forbs primarily dependent on propagation from seed (spotted knapweed), seed and adventitious roots (Russian knapweed), or seed and vigorous sprouting from rhizomes (leafy spurge). To address this objective, we designed an experiment to evaluate the effects of fire fuel load and identify heat regimes required to kill invasive plant seeds deposited on the soil surface. Because fuel load is related to heat release and species vary in seed morphology and fire history, we hypothesized that percentage and probability of emergence would decrease with increasing fuel load and vary by species.

Material and Methods

Experimental Methods. Seeds of Japanese brome, spotted knapweed, Russian knapweed, and leafy spurge were subjected to fire at six fuel loads (100, 200, 300, 400, 500, and 700 g m^{-2}) and a nonburned control using a factorial arrangement with six replications of each species–fuel load combination and pans of seeded soil as experimental units. Seeds were collected locally in the field immediately after ripening. Seeds were stored at 18 C for 6 to 9 mo before the study. Grassland fires were simulated by burning field-cured grass in a cage containing one pan of each species. Time–temperature profiles for the soil surface were collected from a thermocouple in each pan. After fire, pans were immediately placed in a growth chamber[1] to determine percentage emergence.

Duplicated trials with 100 seeds of each species were conducted to determine germination rates before treatment. Seeds were evenly placed on moistened filter paper in 9-cm petri dishes and placed in a seed germinator[2] for 37 d (12-h light at 21 C, 12-h dark at 15 C). Percentage germination was determined by counting the number of seeds with a visible protrusion of the radicle during the 37-d period. A 6-mm hole was drilled through the center of the aluminum pans (178 by 102 mm and 20 mm deep), which were then filled and tamped within 2 mm of the lip with a potting mix consisting of silty loam soil, washed concrete sand, and peat moss in equal parts by volume. On the basis of percentage germination of nontreated seed, 105, 110, 150, or 700 seeds of Japanese brome, spotted knapweed, Russian knapweed, and leafy spurge, respectively, were placed in each pan to obtain 100 germinable seeds per replication. Seeds were evenly distributed on the soil surface, with one species per pan. Pans were not watered before fire treatment.

The fire cage was 1 m long, 0.5 m wide, 0.5 m tall, and elevated 30 cm above ground level. The cage was constructed in a steel frame with 1-cm wire mesh walls and lid and a 3-mm-thick steel plate floor. Four slots were cut in the floor to allow pans to be inset with the top lip flush against the floor and the center of the pan 70 cm from the front edge of the cage, allowing a passing fire front. One pan of each species was randomly placed in each slot for each replicated fire treatment. A type-K thermocouple[3] insulated with ceramic fiber and Inconel braiding was inserted upward through the 6-mm-diam hole in each pan and leads were clamped such that the beads were fixed on the soil surface. Thermocouples were connected to a micrologger with a storage module[4] to record time–temperature profiles at 1-s intervals during treatment. Time–temperature profiles were converted to degree-seconds above a base temperature of 50 C to estimate heat dosage as total exposure to potentially lethal temperatures. Heat dosage data were summarized by thermocouple within burn.

The fuel source was crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] cut from nongrazed stands during late March with a sicklebar mower. After mowing, the grass was raked, dried to a constant weight at 60 C, then weighed to the nearest gram and bagged in 50-, 100-, 150-, 200-, 250-, and 350-g increments. After thermocouples were inserted into pans, the grass was spread on the floor of the cage by hand to ensure visually even distribution. The grass was covered with galvanized wire poultry netting to slightly compress the fuel and reduce movement during fire. Resulting average fuel depths were 2, 3, 4, 6, 7, and 9 cm for the 100 through 700 g m^{-2} fuel load treatments, respectively. A line of fuel (60 : 40 diesel : gasoline) was poured at the edge of the cage and then ignited for an even fire front, and a fan was used to provide a steady rate of spread. After all smoldering had ceased, pans were immediately transported to the growth chamber for emergence trials.

The growth chamber was set for 12-h light and 12-h dark periods, with temperatures ranging from 18 to 24 C. Pans were monitored daily for 54 d when emergence ceased and soils were kept moist with reverse-osmosis water throughout the period. Seedlings were recorded and removed from pans as cotyledons emerged. Data were summarized as percentage of seed and number of seedlings emerged by pan.

Statistical Analyses. Soil surface maximum temperature and degree-seconds above a 50 C base were analyzed with ANOVA (SAS Institute, Inc. 1989) for a completely randomized design with a factorial arrangement of six fuel loads receiving fire and four species. The relationship between fuel load and heat dosage was estimated by regression analysis with the GLM procedure of SAS. Significant differences were declared at $P < 0.05$ and means from significant main and interaction effects were separated using tests of simple effects.

There was an abundance of zeros in the seedling germination data set because of no seedling emergence with many of the heavier fuel loads. These zeros prevented the data from being well-approximated by the normal distribution. Therefore, we used credibility intervals from a Bayesian generalized linear model to estimate relationships between fuel loads and probabilities of germination. The model was fit separately to data on each species. The number of seeds emerging from aluminum pan i (y_i) was taken to be binomially distributed:

$$p(y_i|m,r,t,\sigma) = \binom{n}{y_i} \left(\frac{e^{\eta_i}}{1+e^{\eta_i}} \right)^{y_i} \left(\frac{1}{1+e^{\eta_i}} \right)^{\eta-y_i} \qquad [1]$$
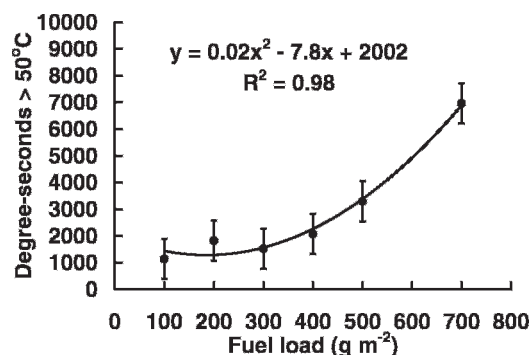
Figure 1. Relationship between fuel load (crested wheatgrass at 3.7% moisture) and degree-seconds above 50 C at the soil surface. Vertical bars represent standard errors of the means.

where n is the number of seeds in the pan, $\eta_i = \log\left(\dfrac{\mu_i}{1-\mu_i}\right)$, and μ_i is the probability of interest; i.e., the probability a seed became a seedling. We assumed the η_i followed a normal linear model:

$$\eta_i = m + r_j + t_k + \varepsilon_i \qquad [2]$$

where m describes the probability of germination in the absence of fire, r_j is the replication j effect, t_k is the fuel load k effect, and $\varepsilon_i \sim N(0, \sigma^2)$.

From a Bayesian perspective, Equations 1 and 2, respectively, form the prior distribution and likelihood function for the η_i. To complete our hierarchical Bayesian model, we assigned a commonly used noninformative prior distribution to the parameters of Equation 2:

$$p\left(m, r, t, \sigma^2 | \mathbf{X}\right) \propto \sigma^{-2}$$

where $\mathbf{X}$ is the design matrix. See Chapter 16 of Gelman et al. (2004) for more details on this model. We used Markov chain Monte Carlo integration to simulate the joint posterior distribution of model parameters for each species. We wrote a Fortran program[5] to perform the integrations.

Results

Fire conditions promoted good combustion of grass fuels, with an ambient temperature of 18 C, consistent air movement at 2 m s^{-1}, 42% relative humidity, and 3.7% fuel moisture. Thermocouple readings were quite variable within individual fires because of minor differences in their proximity to burning grass and variation in smoldering time among patches of fuel. However, there were no differences among species in maximum temperatures ($P > 0.73$) or heat dosage (degree-seconds) at the soil surface ($P > 0.13$) in burned treatments. Maximum temperature was similar across fuel loads ($P > 0.26$), with a mean of 122 ± 11.5 C and a range of fuel load means from 107 to 143 C. Greater fuel loads prolonged active flaming and smoldering, so degree-seconds (above a 50 C base) at the soil surface varied with fuel load ($P < 0.01$) from a mean of 1,138 at 100 g m^{-2} to 6,992 degree-seconds at 700 g m^{-2}. There was a positive quadratic relationship between degree-seconds and fuel load, with fuel load explaining 98% of the variation in mean soil surface degree-seconds across species (Figure 1).
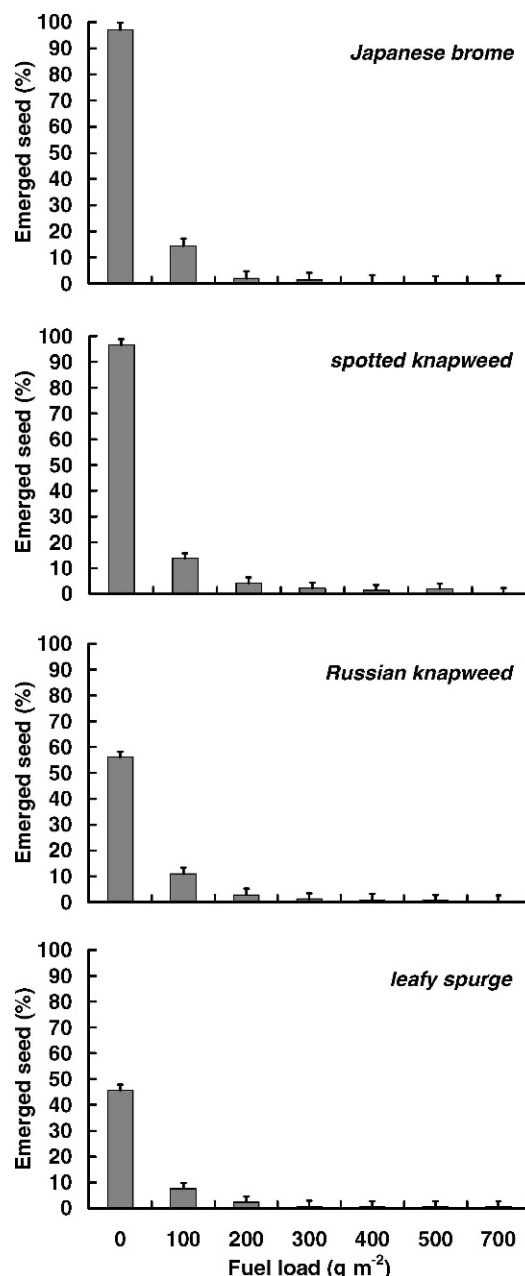

Figure 2. Percentage of Japanese brome, spotted knapweed, Russian knapweed, and leafy spurge seeds germinating and emerging in a nonburned control and following exposure to fire at six fuel loads. Vertical bars represent the standard error of the species-by-fuel load comparisons (2.5%).

Seed densities applied resulted in 102, 106, 84, and 320 ± 8 emerged seedlings in nonburned pans of Japanese brome, spotted knapweed, Russian knapweed, and leafy spurge, respectively. Emergence of Russian knapweed seedlings was less than projected and slower than that of other species, continuing for 14 d after the last seedling emerged for other species. Soil contact appeared to favor leafy spurge seeds, with more than three times the seedlings emerging in pans than were expected on the basis of preliminary tests on filter paper.

In the absence of fire, the sample means for emergence were 97% for Japanese brome and spotted knapweed, 56% for Russian knapweed, and 46% for leafy spurge (Figure 2). Fire at any fuel load reduced percentage emerged seedlings for all species. Exposure to fire with 100 g m^{-2} fuel loads reduced emergence of the four species 80 to 86% relative to

Table 1. Posterior modes (bold) and 95% (2.5–97.5%) credibility intervals (parentheses) on probabilities of invasive plant seedling emergence at seven fire fuel loads.

Fuel load	Posterior mode probability and 95% credibility interval			
	Japanese brome	Spotted knapweed	Russian knapweed	Leafy spurge
(g m^{-2})				
0	**0.983** (0.935–0.996)	**0.984** (0.935–0.997)	**0.671** (0.220–0.941)	**0.422** (0.180–0.711)
100	**0.147** (0.044–0.402)	**0.147** (0.039–0.440)	**0.141** (0.022–0.556)	**0.052** (0.016–0.156)
200	**0.016** (0.003–0.058)	**0.030** (0.007–0.125)	**0.016** (0.001–0.098)	**0.012** (0.004–0.040)
300	**0.009** (0.002–0.039)	**0.012** (0.002–0.056)	**0.009** (0.001–0.062)	**0.005** (0.001–0.017)
400	**0.003** (0.000–0.016)	**0.010** (0.002–0.049)	**0.006** (0.000–0.048)	**0.003** (0.001–0.012)
500	**0.001** (0.000–0.007)	**0.016** (0.003–0.074)	**0.002** (0.000–0.018)	**0.003** (0.001–0.010)
700	**0.002** (0.000–0.013)	**0.000** (0.000–0.000)	**0.002** (0.000–0.020)	**0.004** (0.001–0.014)

nonburned treatment. Sample means for percentage emergence were similar for Japanese brome and spotted knapweed (14.2%), less for leafy spurge (7.6%), and intermediate for Russian knapweed (11.1%). Increasing fuel loads to 200 g m^{-2} reduced emergence 98% relative to nonburned treatment for Japanese brome and 95% for the other species.

Nonoverlapping 95% credibility intervals provided strong evidence that, in the absence of fire, the probability of leafy spurge emergence was less than that for Japanese brome or spotted knapweed (Table 1). However, the probability of a seedling emerging when exposed to fire was similar across species within each fuel load, with one exception. Emergence probability of leafy spurge slightly exceeded the 0.0 probability for spotted knapweed with 700 g m^{-2} of fuel.

Probability of emergence decreased with increasing fuel load (Table 1). Burning a fuel load of 100 g m^{-2} greatly reduced posterior mode probabilities of emergence for all species except Russian knapweed. Credibility intervals were greater at 100 g m^{-2} than those at other fuel loads, in part because such light fuel loads provided gaps in fuel and some refuge from prolonged heat. Posterior mode probabilities were less than 0.01 with 300 g m^{-2} or greater fuel loads for all species but spotted knapweed. Lower limits on probabilities of emergence were 0.0 at the three heaviest fuel loads for Japanese brome and Russian knapweed and the probability was 0.0 for spotted knapweed with 700 g m^{-2}. However, a portion of leafy spurge seeds was expected to emerge at any of the fuel loads tested, even though probabilities were generally less than 0.01.

Discussion

Fire is capable of sharply reducing the probability that soil surface-deposited seeds will germinate and emerge. Reducing the probability a seed will emerge to 0.13, and generally less, by burning 200 g m^{-2} of fine fuel is noteworthy, as many grasslands support equal or greater fuel loads. The relationship between fuel load and seedling emergence also offers considerable predictability of fire effects on four invasive plant species' seeds. Whereas some field studies have observed postfire reductions in weed populations (e.g., MacDonald et al. 2007; Whisenant 1990), these results verify that fire-induced seed mortality is a mechanism by which invasive plant abundance or initial establishment may be reduced and that mortality increases with fuel load (heat dosage). Interestingly, various methods of thermal control have successfully been applied to kill seeds in croplands and hardscapes (Ascard 1998; Rask and Kristoffersen 2007) and beyond the plant kingdom, similar fire effects have been observed with grasshoppers in laboratory and field experiments (Branson and Vermeire 2007; Vermeire et al. 2004). Ultimately, numerous factors will interact to affect fire impact on invasive plants, including fire history of the area relative to invading and indigenous species, fuel and weather conditions, spatial distribution of seeds, and postfire environment. Each of these factors requires consideration to successfully reduce invasive plants with fire.

Plant species that evolved in fire-prone habitats are likely to be fire adapted such that established plants can sprout after fire, or their seeds avoid heat damage. Fire-prone habitats often have species with large seed banks and germination of these species can be promoted by fire through scarification (Gashaw and Michelsen 2002), smoke (Adkins and Peters 2001; Keeley and Fotheringham 1998), or changes in nutrient availability (Pate et al. 1985; Thanos and Rundel 1995). Therefore, fire may be instrumental in the maintenance or restoration of indigenous plant communities with fire-adapted species when invaders are not fire adapted or differences in their adaptations can be targeted. For example, annual spring burning of C$_4$-dominated tallgrass prairie reduced exotic plant richness 80 to 90% because the historic regime is one of frequent fire and 90% of exotics were C$_3$ species with greater exposure of live tissues at the time of fire (Smith and Knapp 1999). Where differences among exotic and indigenous species are less stark, the fire-induced reduction in exotic species may be relatively less, but offset by increased establishment of indigenous species (Gillespie and Allen 2004). In either case, restoration of fire as a continued process rather than a single event is important because initial success has been followed by reinvasion when fire was not repeated (Kyser and DiTomaso 2002). Fire may promote invasion in situations where invasive plants can better avoid damage by fire than the dominant indigenous species, or those where invasive plants alter the fire regime (Brooks et al. 2004). Such is the case with downy brome (*Bromus tectorum* L.) invasion into grasslands and shrublands of the western United States. Downy brome has altered the seasonality of fire and increased fire frequency relative to natural regimes and this has proven detrimental to indigenous bunchgrasses and shrubs (Knapp 1996). Such examples appear to be the exception rather than the rule, particularly in regions where natural fire return intervals are relatively short (Grace et al. 2001).

Fuel and weather conditions can alter combustion, which affects heat transfer. Stinson and Wright (1969) observed maximum temperatures that exceeded those we measured and they noted a strong positive relationship between fuel load and maximum fire temperature. In part, differences occurred because their thermocouples were elevated slightly above the

soil surface, but much of the difference could be attributed to the generally greater ambient temperatures under which Stinson and Wright (1969) burned. The effects of such changes are evident with comparison of our results with those of field experiments examining fire effects on Japanese brome and spotted knapweed. With fuel loads of 211 to 276 g m^{-2}, Whisenant (1990) showed a 94% reduction of the Japanese brome litter seed bank the first year after fire and delayed reductions in the soil surface seed bank of 27 to 63%. The greater reduction (98%) we observed with a 200 g m^{-2} fuel load and similar fire weather conditions may be explained by fuel conditions. Whisenant (1990) had a mixture of dead and young live fuel (18 to 23% water), whereas all of our fuel was dead and dry (3.7% water), allowing for better combustion. Field experiments of fire effects on spotted knapweed also yielded lesser impact on seedling recruitment than our results indicated. Burning into the wind with a mean fuel load of 316 g m^{-2} reduced spotted knapweed seedling density 63% (MacDonald et al. 2007) compared with the 98% reduction we observed with headfires in 300 g m^{-2} of fuel. Wind-driven fires can produce fire intensities an order of magnitude greater than backing fires (Roberts et al. 1988) and our results showed germination to be negatively related to heat dosage through changes in fuel load. Emery and Gross (2005) observed 33 to 78% reductions in spotted knapweed seedling density with fuel loads ranging from 136 to 508 g m^{-2}. Although they did not report fire weather or fuel conditions, Emery and Gross (2005) reported that fires were of relatively low intensity, consuming only 40 to 57% of the biomass. So, although fuel load can provide a good approximation of heat effects, conditions that alter the extent to which fuels combust must be considered as well.

Heat produced by fire will vary vertically and horizontally in a landscape. Whereas our results describe the probability of postfire seedling emergence by fuel load, it is important to recognize that multiple factors including fuel load, fuel condition, topography, and weather will change as a fire front passes. Heat exposure for patches within the landscape then will likely be at least as heterogeneous as the distribution of fuel loads. Generally, nonburied seeds will receive the least heat at the soil surface and greater heat in the canopy, unless they are contained within a portion of the canopy that does not burn and significantly exceeds flame height. Buried seeds will be exposed to less heat as depth in soil increases and may experience no immediate temperature change at depths greater than a few centimeters. Therefore, the ultimate impact of fire on seedling emergence depends on the vertical distribution of seeds and heat transfer through the soil as they interact (Whelan 1995).

Vertical seed positions have been shown to vary with soil physical properties, seed morphology (Chambers et al. 1991), granivore activities (Chambers and MacMahon 1994), and livestock trampling (Rotundo and Aguiar 2004). Presumably, seed longevity will play a role in determining maximum depths for viable seeds as well because the longer a seed is present, the more time it has to become deeply deposited. Seedling emergence tends to be greater for buried seeds in the top centimeter of soil than those on the soil surface, but decreases with increasing depth below the top few centimeters (Chambers 1995; Chauhan et al. 2006; Grundy et al. 1996; Rotundo and Aguiar 2004). Some germinable seeds of the four species we examined have been observed 6 cm and deeper in the soil (Legg et al. 1992; Qinfeng et al. 1998). These species have also been found to have some viable seeds exceeding 7 yr old, but viability decreases sharply the first 2 or 3 yr after deposition (Bowes and Thomas 1978; Davis et al. 1993; Sheley and Petroff 1999). Therefore, the overwhelming majority of viable seeds will generally be found near the soil surface (Chippindale and Milton 1934) and in the litter layer, leaving them vulnerable to fire-induced mortality. Seeds buried in the top 2 cm of soil will be better insulated, but still susceptible to heat damage, depending on fine (< 6-mm-diam) fuel loads. Larger fuels would be required to significantly raise temperatures and extend the duration of heat exposure deeper than 2 cm (Bradstock and Auld 1995).

Effects of the postfire environment must be considered in the application of fire for invasive plant management. Grassland fire is complex in that beyond the immediate direct effects on plant and animal communities, it can have indirect effects as well through changes in energy flow, water and nutrient cycling, and microenvironment that occur across multiple timescales. For example, the temporary reduction in litter and plant cover after fire can have significant ramifications for community response as both have been shown to inhibit germination (Gross et al. 2005; Jutila and Grace 2002) or in arid environments, aid in the establishment of invasive plants (Evans and Young 1970). Sowing native and nonnative plant seeds into burned and nonburned sites, Maret and Wilson (2000) determined that fire increased seedling accumulation of most native species, but some of the nonnative species responded positively as well and the authors cautioned that benefits may depend on the state of invasion at the time of fire. Because the biology of each species is in some ways unique, response to fire and requirements for establishment can be expected to vary by species as well.

Understanding a targeted plant's biology is necessary, but by itself, may not allow for control of invasive plants through fire alone. Rather, successful use of fire in control of invasive species will likely require an integrated management approach. In managing opportunistic species, it is commonly suggested that disturbance and rapid vegetation type conversion be limited (Dodson and Fiedler 2006; Keeley 2006). However, control of some species has been minimal with biological, chemical, mechanical, or fire treatment alone and quite effective when methods were combined (Paynter and Flanagan 2004). Fire provides additional opportunities to disrupt the life cycle of invasive species through direct seed mortality, whereas other methods often affect only established individuals. Manipulating fire behavior to promote high seed mortality then may hasten and improve restoration efforts if coordinated with management that targets invasive individuals surviving fire or different stages of their life cycle.

Sources of Materials

Acknowledgments

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